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Invasive versus native brachyuran crabs in a European rocky intertidal: respiratory performance and energy expenditures

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Abstract

The invasive Asian shore crab *Hemigrapsus sanguineus* is now the second most abundant intertidal crab in the North Sea after the native European green crab *Carcinus maenas*. To compare their respiratory performance and energy expenditures, we measured standard respiration rates of both species from around the island of Helgoland, North Sea, Germany (54°11′N, 7°53′E) in 2015. Oxygen consumption was recorded in a flow-through setup between 5 and 20 °C. At lower temperatures, *H. sanguineus* had similar respiration rates as *C. maenas,* but approximately twofold higher rates at higher temperatures. Numerical models for the calculation of individual respiration rates were established and applied to the entire intertidal populations around Helgoland to compare the energy expenditures of both species. Abundance and biomass data recorded in August 2014 showed that *H. sanguineus* reached values as high as 21 and 59%, respectively, compared to those of *C. maenas*. Based on these data and the numerical respiration models, the energy expenditures of both populations were calculated for the whole year 2014. The *H. sanguineus* population reached, depending on the assumed diet of both species (complete herbivory versus complete carnivory), 86–135% of the expenditure value of *C. maenas*. As population densities of *H. sanguineus* are likely to increase in the North Sea, the energy expenditure of the invader and thus its impact on the energy flux in the intertidal habitat will further increase. Whether this will lead to an impact on the local intertidal community depends on species-specific dietary preferences and remains to be investigated.

Introduction

Biological invaders are generally seen as a major threat to biodiversity in the marine realm (Grosholz 2002). Potentially, they may drastically change the native community structure and the function of an ecosystem. If the ecological impact is high, ultimately, ecosystem services and thus human economic interest and health may be affected (Ruiz et al. 2000; Simberloff et al. 2013).

Species of brachyuran decapods frequently invade coastal and marine ecosystems (Brockerhoff and McLay 2011). Due

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to their pronounced invasion potential, two of these species are relatively well studied: the European green crab *Carcinus maenas* and the Asian shore crab *Hemigrapsus sanguineus*. The first is native to European and African coasts of the North Atlantic. It invaded the coasts of North America by 1817 (Carlton and Cohen 2003). Subsequently, *C. maenas* appeared on coasts all around the world, including the North American Pacific coast, South Africa, Australia, and Japan (Carlton and Cohen 2003). The latter, *H. sanguineus*, is native to Japanese, Korean, and Chinese coasts. It invaded the Atlantic coasts of North America in the late 1980's and the European Atlantic coasts in the late 1990's (Stephenson et al. 2009). On the Atlantic coasts of North America, *H. sanguineus* can be found from Cape Hatteras in North Carolina up to the Schoodic Peninsula in Maine (Williams and McDermott 1990; Delaney et al. 2008; Epifanio 2013). Its current European distribution ranges from the French Atlantic coast to the German Wadden Sea (Dauvin et al. 2009). A few specimens were also reported in the Adriatic Sea, the Black Sea and the Swedish Skagerrak (Schubart 2003; Micu et al. 2010; M. Berggren, Sven Lovén Centre for Marine Sciences—Kristineberg, Fiskebäckskil, Sweden, pers. comm.).

The ecology and physiology of *C. maenas* is well studied (e.g., Crothers 1967; Roman and Palumbi 2004; Breen and Metaxas 2012 and references therein). Ecological information on *H. sanguineus* is growing, mostly from invaded areas, where increasing numbers of *H. sanguineus* share habitats and possibly compete for resources with *C. maenas* (for native areas, e.g., Fukui 1988; Lohrer et al. 2000a; for invaded areas, e.g., McDermott 1998; Jensen et al. 2002; Lohrer and Whitlatch 2002; Epifanio 2013 and references therein; Jungblut et al. 2017). However, physiological data of *H. sanguineus* are rather scarce (Breen and Metaxas 2012) and stem mostly from the invaded US east coast. For instance, the species was identified as an income breeder, meaning that it utilizes energy ingested during reproductive times directly for egg production (Griffen et al. 2012). Furthermore, respiration rates of *H. sanguineus* were not affected by algal diet, however, rates increased with the amount of consumed animal diet due to the increasing costs for digestion (Griffen et al. 2015). In the same study, two condition parameters, hepatosomatic index and hepatopancreas total lipid content, increased with increasing consumption of animal diet, but not with increasing amounts of algal diet.

Respiration, integrating all aerobic metabolic processes of an organism, can serve as a proxy of the energetic impact that an organism has on its environment via food uptake (Brey 2010). These physiological processes include transformation of energy and matter. They require the uptake of O_2 (respiration) and release CO_2 (Ikeda et al. 2000). Hence, respiration rates can be used to calculate carbon uptake, metabolic energy expenditures and, thus, the energetic impact

of an organism on its habitat in terms of food uptake (Ikeda et al. 2000). Body mass of an organism and ambient temperature are the most important predictors for estimating aquatic invertebrate respiration rates (Brey 2010). Models for the calculation of respiration from mass and temperature are available for marine pelagic copepods (Ikeda et al. 2007), for calanoid copepods (Bode et al. 2013), euphausiids (Ikeda 2013), and some decapod species (e.g., Crear and Forteath 2001).

Based on the success of *H. sanguineus* in newly invaded areas, we hypothesized that this species has physiological advantages over the native species *C. maenas*. Furthermore, *H. sanguineus* may take up oxygen at higher rates, and therefore, may also have higher energy expenditures compared to *C. maenas*. Thus, (1) standard respiration rates of both species with regard to biomass, temperature, season, and sex were measured between 5 and 20 °C, the temperature range both species naturally experience in their habitat. Based on these data we (2) established temperature- and mass-dependent respiration models for both species. These models were applied to (3) calculate the energy expenditures of both entire intertidal populations around Helgoland to compare the energetic impact of both crab species on their habitat.

Materials and methods

Origin of animals

Carcinus maenas and *Hemigrapsus sanguineus* were collected in April, June, and August 2015 during low tide at an intertidal site at the southwestern tip ('Kringel') on the island of Helgoland, southern North Sea, Germany (54°10′36.5″N, 7°53′03.3″E). The collection site is wave-exposed and the intertidal is composed of many small and large rocks, boulders, as well as coarse sand patches. Hard structures were covered by small to medium-sized macroalgae. Dominating species were *Ulva* spp., *Enteromorpha* spp., *Fucus serratus*, *Chondrus crispus*, and *Mastocarpus stellatus*. For habitat details refer to Bartsch and Tittley (2004). Monthly mean seawater temperatures were 7.6 ± 0.8 in April, 13.4 ± 0.8 in June and 17.7 ± 0.4 °C in August (mean $\pm$ SD, seawater temperature data of the Helgoland Ferrybox, downloaded from the COSYNA data web portal http://codm.hzg.de/codm/).

Oxygen consumption measurements were conducted with crabs of carapace widths from 10 to 40 mm, as those were most abundant in the intertidal areas (Jungblut et al. 2017). Also, no *H. sanguineus* specimen was found with a carapace width above 40 mm. To keep both datasets comparable by individual mass, no *C. maenas* above 40 mm were used.

Throughout their molt cycle, *C. maenas* change their carapace color from greenish to reddish and alter behavior and physiology (reviewed by Styrishave et al. 2004). Red color morphs of *C. maenas* showed a higher oxygen uptake rate than green ones (Reid and Aldrich 1989). As red color morphs of *C. maenas* are very rare in the Helgoland inter-tidal, they were not considered in this study. Moreover, molting and ovigerous decapod crabs showed higher respiration rates (e.g., Lewis and Haefner 1976; Naylor et al. 1997). Therefore, we only included crabs in the inter-molt phase with hard carapaces and we excluded ovigerous females. Very few individuals, which molted during the respiration measurements, were also excluded from the analysis.

Respirometer

Oxygen consumption of the crabs was measured with a custom-built flow-through respirometer (Fig. 1a) installed on a movable laboratory trolley. Temperature-controlled aerated seawater flowed from a 100-L tank through the supply hose passing an oxygen-sensitive and fluorescent foil glued to the inner side of an acrylic holder (Fig. 1b, inflow measuring point). Thereafter, the tube branched out to supply eight cylindrical acrylic glass respiration chambers of approx. 475 mL or, in case of crabs with a carapace width < 15 mm, approx. 190 mL volume (Fig. 1c). Behind each chamber, the water passed another oxygen-sensitive foil (outflow measuring point), a hose pump, and was directed to the sink. Each acrylic holder had a fiber-optic cable placed directly opposite of the oxygen-sensitive foil. The cable transmitted a light impulse from a 10-channel Fiber-Optic Oxygen Meter

(OXY-10, PreSens, Precision Sensing GmbH, Regensburg, Germany) to the foil and the emitting light back to the device. A laptop computer recorded the phase angle shifts between impulse and signal, which depended on the seawater oxygen concentration in the nine measurement channels used (one entrance and eight exit measuring points). The recording software transformed the phase angle shifts to oxygen concentrations.
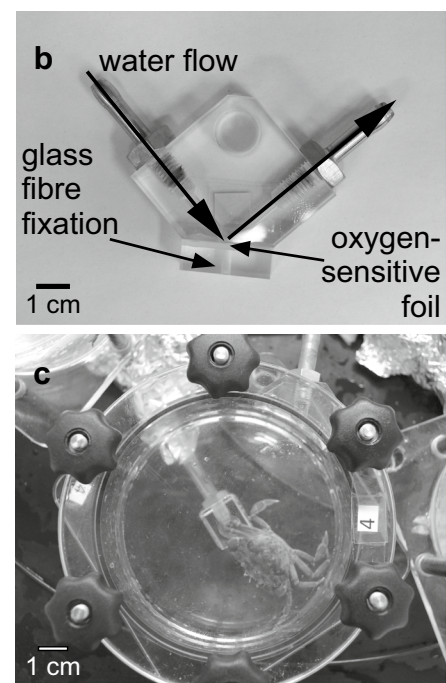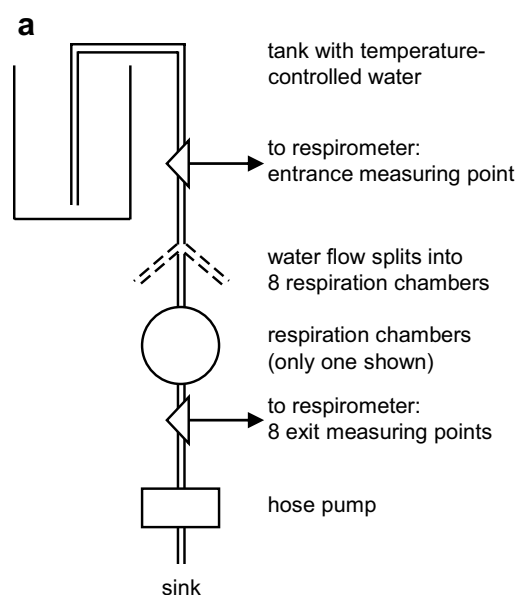
The oxygen meter was calibrated with fully aerated and oxygen-free seawater at a given temperature and salinity. Prior to starting a new series of measurements, the new temperature value was entered into the recording software to adjust the oxygen concentration values. Salinity was the same during calibration and measurements and did not need to be adjusted.

Respiration measurements

After sampling, the crabs were immediately transferred to the laboratories of the Marine Station and kept for 24 h in plastic aquaria in the dark at 10 °C and a salinity of approx. 32.5 to standardize hunger levels and to let the crabs clear their gut. The carapace width of each crab was measured with Vernier calipers to the nearest 0.5 mm. The animals were carefully blotted dry with paper towels for 10 s and weighed to the nearest 0.001 g to obtain their fresh mass.

Each set of measurements (seven crabs and a random control) was performed at consecutively increasing temperatures of 5, 10, 15, and 20 °C. The laboratory trolley with the respirometer was gently rolled into the respective temperature-controlled room, aeration in the supply tank was

Fig. 1 Custom-designed respirometer, **a** water flow during respiration measurements. Tubes between the two measuring points were gas-tight, **b** acrylic holder for oxygen-sensitive foil and **c** respiration chamber with *Carcinus maenas* inside. (photos: S. Jungblut)

a

tank with temperature-controlled water

to respirometer: entrance measuring point

water flow splits into 8 respiration chambers

respiration chambers (only one shown)

to respirometer: 8 exit measuring points

hose pump

sink

b water flow

glass fibre fixation

1 cm

oxygen-sensitive foil

c

1 cm

switched off, and the supply hose of the respirometer was connected to the tank. The seawater used for the measurements had a salinity of approx. 32.5 and never deviated more than ± 0.5 °C from the target temperature. Oxygen concentration measurements were performed once a minute for 8 h per temperature.

Initial gut clearance and the actual measurements took place in the dark to avoid visual stimuli of the crabs, i.e., seeing other crabs through the transparent respiration chambers. Furthermore, oxygen consumption was lower and thus closer to the resting metabolic rates in darkness compared to measurements under the natural light/dark conditions in other intertidal *Hemigrapsus* species (Dehnel 1958).

In preliminary experiments, the required flow rates for different sizes of crabs were determined to avoid oxygen concentrations below 70%. These experiments showed that within 3 h, oxygen concentration readings reached a plateau. This indicates that the water temperature in the respiration chambers had adjusted and the crabs had acclimated to the new temperature. Thus, these first 3 h of each measurement were omitted to account for handling stress and temperature acclimation of the crabs. The remaining 5 h of data collection provided about 300 measurements per crab and temperature.

In total, 63 *C. maenas* (31 males, 32 females) and 64 *H. sanguineus* (32 males, 32 females) were measured at the four different temperatures.

Data processing

Differences between the seawater oxygen concentrations at the joint inflow and at the outflow of each respiration chamber were calculated. These oxygen consumption rates were corrected for unspecific signal fluctuation from the control chamber and values were standardized to the fresh mass of the respective crab.

Data were processed and figures were produced with the GraphPad Prism software (version 5.03). For each set of about 300 measurements per crab and temperature, a frequency distribution with bin width 1 and lower limit 0 was established. Natural logarithms of the minimum, median, and maximum values of these frequency distributions were used to obtain linear regressions between mass-specific respiration and crab mass for each incubation temperature. These linear regressions were used to calculate individual respiration rates of standardized crabs of 0.5, 5, and 10 g fresh mass at each temperature. The minimum values, i.e., the smallest measured value per crab, represent the standard or resting respiration rates. For these, the Q_{10} temperature coefficients were calculated with van't Hoff's generalization:

$$Q_{10} = (R_2/R_1)^{10(T_2 - T_1)},$$

R_1 and R_2 are the metabolic rates, in this case respiration rates, and T_1 and T_2 the corresponding temperatures (Ikeda et al. 2000; Willmer et al. 2000).

Statistical analysis and respiration models

The standard respiration rates, calculated as daily oxygen uptake, were modelled as a function of the following main effects: species (*C. maenas* and *H. sanguineus*), month (April, June, and August), sex (male and female), temperature (5, 10, 15, and 20 °C as a covariate) and individual fresh mass (as covariate). During the modelling the factors sex and month were found to be insignificant for the different crab groups (see section "Results") and these factors were omitted from the model. Empirical regression models were described in detail for zooplankton organisms. In these models, R represents the respiration rate, m the individual's biomass and T the temperature. Derived from the empirical relationships between respiration and biomass, $R = a \cdot m^b$ and $R = c \cdot d^T$ (with a, b, c, d as constants), the regression model is as follows:

$$\ln R = a^0 + a^1 \times \ln m + a^2 \times T,$$

(e.g., Ikeda 1985; Ikeda et al. 2007; Bode et al. 2013; Ikeda 2013). In the main model, all factors were included. For the establishment of the respiration models, however, we constructed two species-specific models, which only included the factors mass and temperature. All statistical models were fitted in R, version 3.2.3 (R Development Core Team 2015) using the functions 'lmer' from the package 'lme4' (Bates et al. 2015) and 'lm' from the generic stats package for the reference models. In all models, we checked the following diagnostics for model stability: Cook's distance and mdffits from the package 'HMLdiag' for lmerMod class objects in R (Loy and Hofmann 2014). In all models, the checks confirmed the absence of influential cases.

Main model

The main model included three interactions of first order: we combined species with either sex, temperature or ln body mass, to test, whether these three factors were affecting respiration differently in the two species.

Each individual was measured consecutively at each of the four temperatures. Since these measurements represent longitudinal data, and consecutive data points are dependent data, we treated temperature as a within-subject's factor and included temporal nesting into the model by including a random factor, where individual is nested in time. Although the factor month was non-significant, the individuals used in the present experiment were still collected in three seasonally distinct batches. Hence, it seems reasonable to include 'month' as a random factor

to control for any grouping effects over season. Because the temporal nesting was individual-specific, the seasonal grouping effect was already accounted for by the random nested term. For the model defined above, the choice of a general linear mixed effects model (LMM) was most appropriate.

We fitted the model using the maximum-likelihood method. With the ln-transformed response variable (see above) we met the assumptions of normal distribution. The variances of the residuals were slightly skewed but within acceptable ranges to meet the assumptions and accept the model. To establish the significance of individual terms, we conducted likelihood ratio tests (LRT) using the R-function 'anova' with the argument 'test' set to 'F'. Hereby, we compared the deviances of the respective full model with the corresponding reduced model not comprising the respective factor and/or term of interest. When testing for main factors, which were combined into a random factor, we created reference models, from which we omitted the respective random factors and subsequently applied the LRT for our term of interest (e.g., species and temperature). Non-significant interactions and terms were removed from the previous full model (main factors sex and month, see 'Results').

Respiration models

The data were also used to establish mass- and temperature-specific respiration models for *C. maenas* and *H. sanguineus*. Therefore, we separated the final model into two species-specific models. Both included only the main factors temperature and ln of mass (which were shown to be the significant main factors), as well as the random within-subjects-factor (individual nested in temperature). The coefficients of each model were then used to establish a respiration model for rates of the two individual species from habitats, where information on temperature and biomass was available. Thereby, however, we used only the coefficients of the fixed effects (i.e., intercept and slopes for temperature and mass), which could then be multiplied with empirical measurements of temperature and ln of mass. For the final predictions in the actual scale, the inverse natural exponential function was applied to the ln-transformed predictions. We omitted the random term (subject nested in temperature) in the equation for the calculations of respiration rates, because they are only relevant for the present experimental design. In fact, future data might be collected in other months than those given in the present model. In addition, the estimates should not be specific for individual animals that were used in the present experiment, but should reflect individuals of a certain species in general.

Energy expenditures of the Helgoland crab populations

We assessed the energetic impact of the *C. maenas* and *H. sanguineus* populations onto their rocky intertidal habitat around the island of Helgoland via their food uptake, similar to a procedure used by Hu et al. (2012). Population respiration and energy expenditures were calculated based on the respiration models developed in this study, as well as the abundance and biomass data of both species from the four main intertidal sites in August 2014 (Table 1). For the calculation of a crab's energy expenditure, each individual was assigned its theoretical species-specific standard respiration via the respective respiration model. The average seawater temperature in August 2014 was 18.4 ± 0.8 °C (mean $\pm$ SD, seawater temperature data of the Helgoland Ferrybox downloaded from the COSYNA data web portal http://codm.hzg.de/codm/). Considering its mass, the total daily respiration of each crab was calculated. By multiplication with the respiratory coefficient, the daily respiration was transformed into the daily CO_2 release (Gnaiger 1983). Respiratory coefficients depend on the ingested food and range from 1 (herbivory) to 0.8 (carnivory) (Willmer et al. 2000). Since the feeding preferences of both species are not yet clear around Helgoland, we calculated the daily energy expenditure for both extremes. The daily CO_2 release was multiplied by the molar mass of carbon (12 g mol^{-1}) to obtain the daily carbon uptake. As 1 g organic carbon equals 41.4 kJ stored energy (Salonen et al. 1976), the daily metabolic energy expenditure E (kJ d^{-1}) for each crab can be calculated:

$$E = R \times m \times RQ \times 12 \times 10^{-6} \times 41.4,$$

with R (µmol g^{-1} d^{-1}) as the previously calculated respiration rate of the crab, the crab's body mass m (g) and the respiratory quotient RQ (ratio, no unit). By summing up all of the individual energy expenditure values per species, the daily energy expenditure was calculated per square meter and day for each of the four main intertidal sites around Helgoland. Multiplying these values with the spatial area of each site, the total energy expenditures of each species for each site were calculated. Therefore, the spatial areas (excluding large tide pools and concrete blocks) of the four main sites were established on the basis of the GIS map published by Bartsch and Tittley (2004) (H. Pehlke, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany, pers. comm.). Summing up the four energy expenditure values resulted in two species-specific values for the whole Helgoland intertidal area.

In the same way as described above, we calculated the metabolic energy expenditure for the other months and the cumulative value of the year 2014 for both species. The calculations used monthly means of seawater temperature for the respiration models (seawater temperature data of the

Table 1 Abundance and biomass of *Carcinus maenas* and *Hemigrapsus sanguineus* in August 2014 (from Jungblut et al. 2017) as well as spatial areas of intertidal sites around the island of Helgoland, Germany (areas established on the basis of the GIS map from Bartsch and Tittley 2004)

Sites (sensu Jungblut et al. 2017)	Sites and habitats (sensu Bartsch and Tittley 2004)	Total area (m²)	Abundance				Biomass			
			C. maenas		H. sanguineus		C. maenas		H. sanguineus	
			(ind. m⁻²)	Total (ind.)	(ind. m⁻²)	Total (ind.)	(g m⁻²)	Total (kg)	(g m⁻²)	Total (kg)
Northwestern	Wave-cut platforms NE and W; red sandstone ridges, boulder fields	145,207	26.0	3,775,382	3.3	479,183	17.1	2483.0	8.4	1219.7
Northeastern	Boulder field east of 'beach N'	763	14.3	10,911	40.3	30,749	23.3	17.8	88.8	67.8
Southwestern	'Kringel' area; red sandstone ridge with boulders	37,255	59.0	2,198,045	19.3	719,022	53.3	1985.7	35.9	1337.5
Southeastern	Boulder field south of 'landing pier'	2396	17.0	40,732	16.0	38,336	11.6	27.8	24.2	57.9
Total		185,621		6,025,070		1,267,290		4514.3		2682.9

lightship "German Bight" downloaded from the COSYNA data web portal http://codm.hzg.de/codm/). In contrast to the abundance and biomass data of both crab species from August 2014 (Table 1), only semi-quantitative data of *C. maenas* abundance were available for the Helgoland intertidal from the mid-1980s (Janke 1986). As the latter data are relatively old and *H. sanguineus* was not present in the Helgoland area at that time, the calculations were based on the data from August 2014. However, Janke (1986) described an absence of *C. maenas* from the Helgoland intertidal areas from November to February, due to migration to subtidal areas. This phenomenon was also described for Danish waters (Aagaard et al. 1995) and was again recently observed for Helgoland (S. Jungblut, pers. obs.). Therefore, *C. maenas* was excluded from the calculations for the 4 months of absence, as this species does not contribute to the energy flux in the intertidal during this period. In contrast, *H. sanguineus* is present in the intertidal year-round (S. Jungblut, pers. obs.) and was included in the calculations also during winter.

Results

Oxygen consumption

Respiration rates were measured in April, June, and August 2015. No seasonality effect was apparent, when both species were tested together (LRT_{Month}: $df = 2$, $\chi^2 = 3.8308$, $p = 0.147$) and when *Carcinus maenas* was treated separately (LRT_{Month}: $df = 2$, $\chi^2 = 1.9637$, $p = 0.375$). For *Hemigrapsus sanguineus*, however, the result revealed a seasonality effect, yet on the verge of the significance level (LRT_{Month}: $df = 2$, $\chi^2 = 6.2533$, $p = 0.044$). Differences between sexes and interactions between sexes and species were not significant (LRT_{Sex}: $df = 1$, $\chi^2 = 2.4089$, $p = 0.121$ and $LRT_{Sex \times Species}$: $df = 1$, $\chi^2 = 1.0362$, $p = 0.3087$).

Overall, the native *C. maenas* specimens showed higher respiration rates than the non-native *H. sanguineus* ($LRT_{Species}$: $df = 1$, $\chi^2 = 22.056$, $p < 0.0001$), and both species showed an increase in respiration with increasing temperatures ($LRT_{Temperature}$: $df = 1$, $\chi^2 = 89.724$, $p < 0.0001$) (Fig. 2). The interaction between species and temperature was determined as the only relevant interaction, revealing that respiration rates increased with temperature at a higher rate in *H. sanguineus* than in *C. maenas* ($LRT_{Species*Temperature}$: $df = 1$, $\chi^2 = 13.965$, $p = 0.0002$). Furthermore, respiration rates were negatively related with body mass (LRT_{Mass}: $df = 1$, $\chi^2 = 57.493$, $p < 0.0001$). Respiration rates were mostly dependent on temperature and mass and less on species or the interaction between species and temperature.
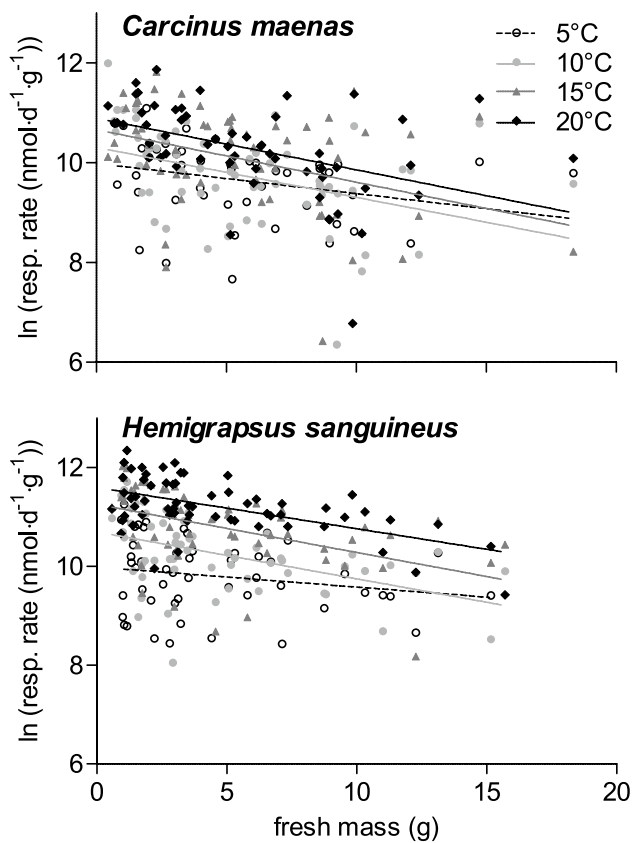
Fig. 2 Standard respiration rates for *Carcinus maenas* (*n* = 63 ind.) and *Hemigrapsus sanguineus* (*n* = 64 ind.) at 5, 10, 15, and 20 °C. The equations of the linear regressions for standard, median, and maximum values of the frequency distributions are presented in Table 2. Original oxygen consumption data and the minimum (= standard), median, and maximum values for the frequency distributions of the original data are presented in the Supplementary Material

Linear regression lines between the crab's fresh mass and the natural logarithm of the corresponding respiration rates were parallel for measurements at 10, 15, and 20 °C and increased with increasing temperatures. Only the regression slope of measurements at 5 °C were less steep in both species (Table 2, Fig. 2).

The specific standard respiration rates of the mass-standardized crabs increased with temperature and decreased with body mass (Fig. 3, Table 3). At 5 and 10 °C, rates were similar in both species at all sizes, whereas at 15 and 20 °C rates of *H. sanguineus* were higher than those of *C. maenas*. Overall, the Q_{10} values for the standard respiration of *H. sanguineus* were higher than those of *C. maenas* (Table 4). Maximal respiration of both species was similar and thus the range between standard and maximal respiration higher for *C. maenas* than for *H. sanguineus* (Fig. 3). In *C. maenas*, the median respiration level was closer to the standard respiration, whereas in *H. sanguineus* it was closer to the maximal respiration.

Respiration models

In the two species-specific respiration models, *R* represents the individual respiration rate (nmol g^{-1} d^{-1}), *m* the crab's body mass (fresh mass, g) and *T* the environmental temperature (°C):

(a) $\ln R = 10.05 + (-0.50 \times \ln m) + (0.05 \times T)$ for *C. maenas*

(b) $\ln R = 9.76 + (-0.38 \times \ln m) + (0.10 \times T)$ for *H. sanguineus*.

The resulting Q_{10} values of the models were independent of mass and temperature and were 1.65 for *C. maenas* and 2.72 for *H. sanguineus*.

Table 2 Regression parameters of standard, median, and maximum mass-dependent respiration measurements of *Carcinus maenas* and *Hemigrapsus sanguineus* at different seawater temperatures: *m* represents the crab's fresh mass (g) and *R* the corresponding respiration rate (nmol d^{-1} g^{-1})

Temperature (°C)	Respiration	C. maenas	H. sanguineus
5	Standard	$\ln R = -0.060 \times m + 9.98$	$\ln R = -0.041 \times m + 9.99$
	Median	$\ln R = -0.095 \times m + 10.71$	$\ln R = -0.044 \times m + 10.59$
	Maximum	$\ln R = -0.076 \times m + 11.27$	$\ln R = -0.049 \times m + 11.06$
10	Standard	$\ln R = -0.100 \times m + 10.31$	$\ln R = -0.095 \times m + 10.70$
	Median	$\ln R = -0.084 \times m + 10.98$	$\ln R = -0.097 \times m + 11.15$
	Maximum	$\ln R = -0.068 \times m + 11.40$	$\ln R = -0.094 \times m + 11.42$
15	Standard	$\ln R = -0.105 \times m + 10.66$	$\ln R = -0.097 \times m + 11.25$
	Median	$\ln R = -0.065 \times m + 11.21$	$\ln R = -0.092 \times m + 11.72$
	Maximum	$\ln R = -0.066 \times m + 11.90$	$\ln R = -0.097 \times m + 11.94$
20	Standard	$\ln R = -0.103 \times m + 10.89$	$\ln R = -0.083 \times m + 11.59$
	Median	$\ln R = -0.039 \times m + 11.44$	$\ln R = -0.079 \times m + 11.94$
	Maximum	$\ln R = -0.062 \times m + 12.20$	$\ln R = -0.090 \times m + 12.17$

Fig. 3 Specific standard, median, and maximum respiration rates of mass-standardized *Carcinus maenas* and *Hemigrapsus sanguineus* of 0.5, 5.0, and 10.0 g fresh mass. The rates were calculated from the regressions of respiration measurements at 5, 10, 15, and 20 °C (Table 2). Error bars represent 95% confidence intervals. The equations of the third order polynomial functions (dashed lines) are presented in Table 3
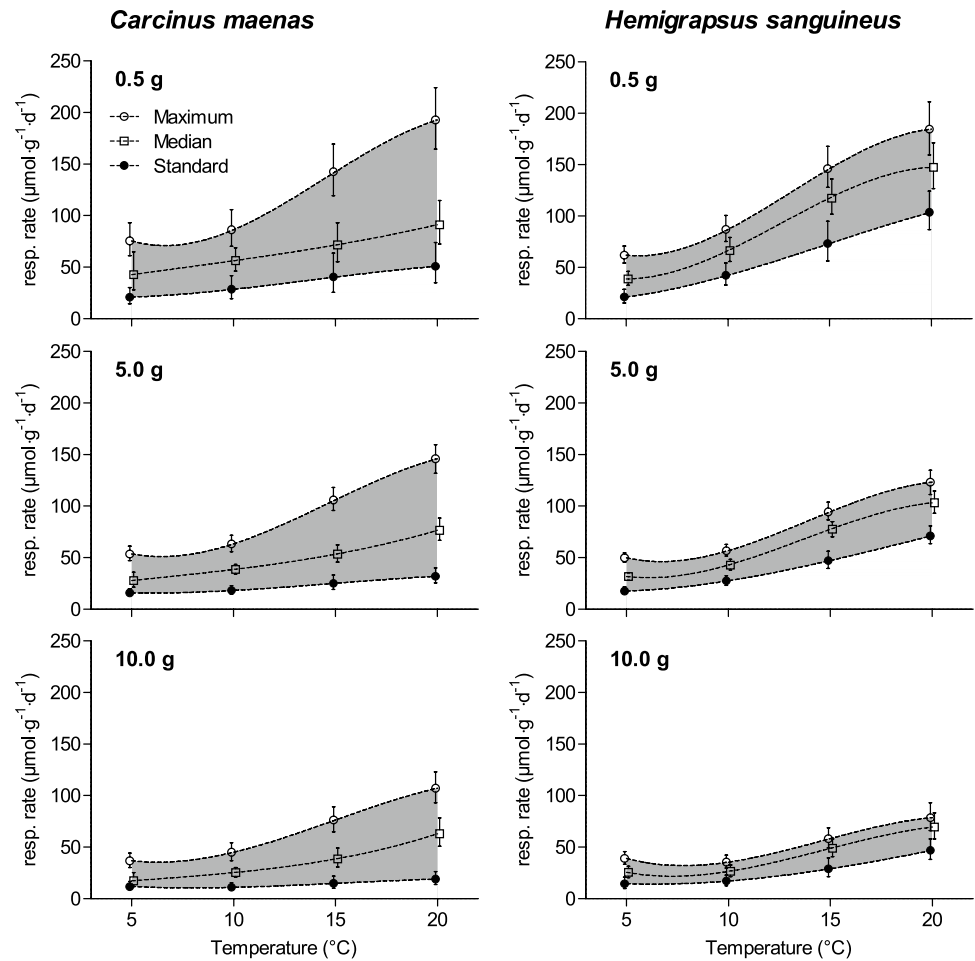
Table 3 Parameters of the fitted mass-dependent third order polynomial models for standard, median, and maximum respiration rates R ($\mu mol\ d^{-1}\ g^{-1}$) of *Carcinus maenas* and *Hemigrapsus sanguineus* depending on temperature T (°C)

Mass (g)	Respiration	C. maenas	H. sanguineus
0.5	Standard	$R = 23.36 + (-1.84) \times T + 0.31 \times T^2 + (-0.01) \times T^3$	$R = 20.55 + (-2.59) \times T + 0.62 \times T^2 + (-0.01) \times T^3$
	Median	$R = 28.09 + 3.22 \times T + (-0.08) \times T^2 + 0.003 \times T^3$	$R = 80.26 + (-18.16) \times T + 2.28 \times T^2 + (-0.06) \times T^3$
	Maximum	$R = 161.50 + (-30.28) \times T + 2.96 \times T^2 + (-0.07) \times T^3$	$R = 126.40 + (-25.44) \times T + 2.88 \times T^2 + (-0.07) \times T^3$
5.0	Standard	$R = 23.45 + (-2.78) \times T + 0.29 \times T^2 + (-0.01) \times T^3$	$R = 23.04 + (-2.95) \times T + 0.41 \times T^2 + (-0.01) \times T^3$
	Median	$R = 17.06 + 2.45 \times T + (-0.09) \times T^2 + 0.01 \times T^3$	$R = 76.82 + (-16.75) \times T + 1.77 \times T^2 + (-0.04) \times T^3$
	Maximum	$R = 112.30 + (-20.92) \times T + 2.08 \times T^2 + (-0.05) \times T^3$	$R = 113.20 + (-22.35) \times T + 2.20 \times T^2 + (-0.05) \times T^3$
10.0	Standard	$R = 21.48 + (-3.10) \times T + 0.26 \times T^2 + (-0.01) \times T^3$	$R = 23.99 + (-3.34) \times T + 0.31 \times T^2 + (-0.004) \times T^3$
	Median	$R = 8.59 + 2.22 \times T + (-0.13) \times T^2 + 0.01 \times T^3$	$R = 69.27 + (-14.74) \times T + 1.36 \times T^2 + (-0.03) \times T^3$
	Maximum	$R = 74.93 + (-13.83) \times T + 1.40 \times T^2 + (-0.03) \times T^3$	$R = 98.06 + (-19.25) \times T + 1.69 \times T^2 + (-0.04) \times T^3$

Energy expenditures of the Helgoland crab populations

The respiration models were used to calculate standard respiration and energy expenditures of the intertidal populations of *C. maenas* and *H. sanguineus* around the island of Helgoland, Germany, in August 2014. Total abundance

and biomass of *H. sanguineus* around Helgoland comprised about 21 and 59% of the values for *C. maenas*, respectively (Table 1).

Depending on the animal density, respiration rates of the *C. maenas* population varied from 0.5 to 1.8 mmol O_2 m^{-2} d^{-1} and those of the *H. sanguineus* population ranged from 0.6 to 6.3 mmol O_2 m^{-2} d^{-1} (Table 5).

Table 4 Q_{10} values for standardized *Carcinus maenas* and *Hemigrapsus sanguineus* specimens of 0.5, 5.0, and 10.0 g fresh mass, calculated from respiration measurements at 5, 10, 15, and 20 °C

Mass (g)	Temperature (°C)	Q_{10} C. maenas	Q_{10} H. sanguineus
0.5	5–10	1.86	3.92
	10–15	2.00	3.00
	15–20	1.59	2.00
5.0	5–10	1.30	2.41
	10–15	1.92	2.94
	15–20	1.62	2.27
10.0	5–10	0.87	1.40
	10–15	1.82	2.89
	15–20	1.65	2.61

Total respiration of the entire intertidal crab populations around Helgoland was similar for both species, each accounting for about 201 mol O_2 d^{-1}. Assuming a carnivorous diet (RQ = 0.8), the carbon uptake rates of *C. maenas* population varied from 4.9 to 17.0 mg C m^{-2} d^{-1}. For the *H. sanguineus* population the values ranged between 5.8 and 60.4 mg C m^{-2} d^{-1}. On the basis of a herbivorous diet (RQ = 1.0), the carbon uptake rates varied from 6.1 to 21.3 mg C m^{-2} d^{-1} and 7.3 to 75.4 mg C m^{-2} d^{-1} for the *C. maenas* and *H. sanguineus* populations, respectively. For the entire Helgoland intertidal, carnivorous *C. maenas* would consume about 1933 g C d^{-1}, whereas herbivorous *C. maenas* would ingest about 2417 g C d^{-1}. The daily carbon uptake of *H. sanguineus* would amount to about 1927 g C d^{-1} in case of a carnivorous diet and to 2409 g C d^{-1} in case of a purely herbivorous diet (Table 5). Correspondingly, the population energy expenditures varied from 0.2 to 0.7 kJ m^{-2} d^{-1} for carnivorous *C. maenas* and 0.3 to 0.9 kJ m^{-2} d^{-1} for herbivorous *C. maenas*. The *H. sanguineus* population requires between 0.2 and 2.5 kJ m^{-2} d^{-1} and 0.3 and 3.1 kJ m^{-2} d^{-1}, being either carnivorous or herbivorous (Table 5). For the whole intertidal area of Helgoland, the total energy expenditures amounted to 80,038 and 79,790 kJ d^{-1} for carnivorous *C. maenas* and *H. sanguineus*, respectively. In the case of herbivorous crabs, the corresponding values are higher: 100,047 and 99,738 kJ d^{-1} for *C. maenas* and *H. sanguineus*, respectively (Table 5). The total energy expenditure of the *H. sanguineus* population in August 2014 was thus between 80 and 125% of the value for the *C. maenas* population.

The trends of the energy expenditures of both crab populations resemble the temperature trend during the course of the year (Fig. 4). While in spring the energy expenditure of the *H. sanguineus* population is lower than that of the *C. maenas* population, values are similarly high in summer and autumn. Calculated cumulatively, the energy expenditure of

the *C. maenas* population started after winter, but increased as fast as that of *H. sanguineus* over the year and both were similar at the end of the year (Fig. 4). Depending on the feeding mode, the *C. maenas* population required between 16,040 and 20,050 MJ per year, whereas the *H. sanguineus* population consumed between 17,314 and 21,643 MJ per year. Thus, the cumulative energy expenditure of the *H. sanguineus* population reached 86–135% of the value for the whole *C. maenas* population for the whole year 2014, depending on the preferred diet of either species.

Discussion

### Respiration-temperature dependence

Both species, *Carcinus maenas* and *Hemigrapsus sanguineus*, showed no significant difference in respiration between sexes. Similarly, no pronounced respiratory differences were observed between seasons, as for example noted for Northern krill *Meganyctiphanes norvegica* from the Ligurian Sea, Mediterranean (Saborowski et al. 2002). The significance level that *H. sanguineus* showed with regard to seasonality is, compared to other statistical results, rather vague. Overall, respiration rates resembled those of other brachyuran crabs, e.g., *Ovalipes punctatus*, *Callinectes sapidus*, *C. maenas*, *Hemigrapsus takanoi* (Du Preez 1983; Houlihan et al. 1990; Booth and McMahon 1992; Robertson et al. 2002; Shinji et al. 2009).

Respiration rates of *C. maenas* and *H. sanguineus* differed significantly in their relations between animal size and temperature. Both species showed the classical inverse exponential correlation between mass-specific respiration and body mass known as 'allometric scaling' (e.g., Du Preez 1983; Cockcroft and Wooldridge 1985; Booth and McMahon 1992; Robertson et al. 2002; Brey 2010). They also followed the classical thermodynamic relationship between standard respiration and temperature that describes an exponential increase of oxygen consumption (e.g., Frederich and Pörtner 2000; Saborowski et al. 2000; Pörtner 2002; Verberk et al. 2016). The maximum of this relationship and the subsequent drop of respiration rates beyond the critical temperature due to biochemical and biophysical limitations was not reached in either species. However, the temperature correlation was steeper in *H. sanguineus*, which was also reflected in generally higher Q_{10} values. This may indicate an adaptation to warmer temperatures. For instance, higher oxygen consumption and Q_{10} values were found in warm-acclimated specimens of North Sea isopods (Salomon and Buchholz 2000). In contrast, lower Q_{10} values, as found for *C. maenas*, may be an adaptation to stabilize metabolic rates (Clarke

Table 5 Respiration, carbon uptake and energy expenditure of the intertidal populations of *Carcinus maenas* and *Hemigrapsus sanguineus* at four sites around the island of Helgoland in August 2014

Sites (sensu Jung-blut et al. 2017)	Population respiration per m² (mmol O₂ m⁻² d⁻¹)		Population carbon uptake (for RQ = 0.8) per m² (mg C m⁻² d⁻¹)		Population carbon uptake (for RQ = 1.0) per m² (mg C m⁻² d⁻¹)		Population energy expenditure (for RQ = 0.8) per m² (kJ m⁻² d⁻¹)		Population energy expenditure (for RQ = 1.0) per m² (kJ m⁻² d⁻¹)	
	C. maenas	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*
Northwestern	0.9	0.6	8.8	5.8	11.0	7.3	0.4	0.2	0.5	0.3
Northeastern	0.6	6.3	5.3	60.4	6.6	75.4	0.2	2.5	0.3	3.1
Southwestern	1.8	2.8	17.0	26.5	21.3	33.2	0.7	1.1	0.9	1.4
Southeastern	0.5	2.0	4.9	19.1	6.1	23.9	0.2	0.8	0.3	1.0

	Total (mol O₂ d⁻¹)		Total (g C d⁻¹)		Total (g C d⁻¹)		Total (kJ d⁻¹)		Total (kJ d⁻¹)	
	C. maenas	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*	*C. maenas*	*H. sanguineus*
Northwestern	133.7	88.2	1283.3	847.2	1604.1	1059.0	53,127	35,074	66,409	43,842
Northeastern	0.4	4.8	4.0	46.0	5.1	57.6	168	1906	201	2383
Southwestern	66.1	103.0	634.3	988.3	792.8	1235.4	26,258	40,917	32,823	51,146
Southeastern	1.2	4.8	11.7	45.7	14.6	57.1	485	1893	606	2366
Total	201.4	200.8	1933.3	1927.3	2416.6	2409.1	80,038	79,790	100,047	99,738

Carbon uptake and energy expenditures were calculated for respiratory quotients of RQ = 0.8 (pure carnivory) and RQ = 1.0 (pure herbivory)

Population energy expenditure

Cumulative population energy expenditure
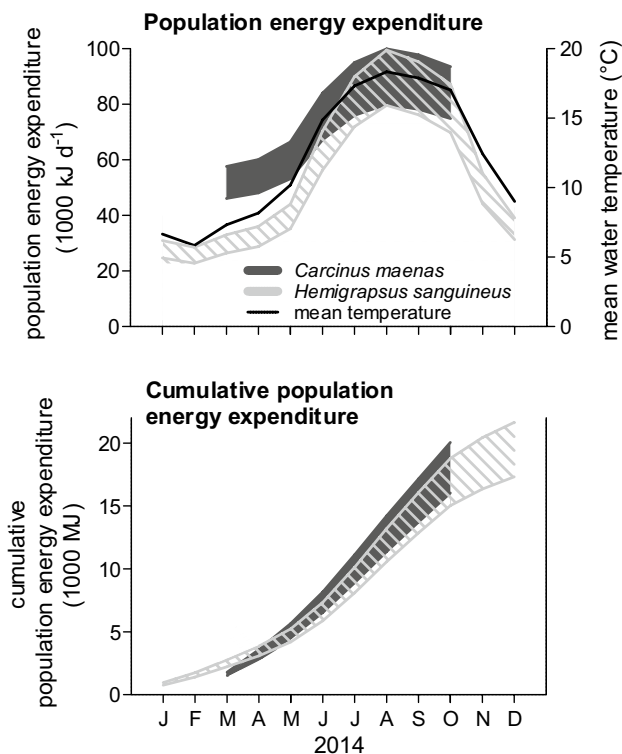
Fig. 4 Population energy expenditure of *Carcinus maenas* and *Hemigrapsus sanguineus* and mean seawater temperatures around Helgoland in 2014, per month and cumulatively. Energy expenditures were calculated for respiratory quotients of 0.8 and 1.0 (pure carnivory and herbivory, i.e., lower and upper margin of each band, resp.)

1983) and may partially explain the worldwide success of *C. maenas* as an invasive species in physically diverse habitats.

Behavior and movements of the crabs were not controlled during the measurements. Therefore, respiration rates above the minimal respiration reflect a combination of standard and routine metabolism, most likely due to enhanced physical activity (e.g., Du Preez 1983). The range between standard and maximum respiration at higher temperatures is wider in *C. maenas* than in *H. sanguineus*, indicating an enhanced potential for occasional bursts of activity in this species. Such activity bursts might be more balanced and probably more frequent in *H. sanguineus*, as its median rates are closer to its maximal respiration rates. Several studies provide evidence of a generally higher agility and activity of *H. sanguineus* compared to *C. maenas*. The invasion of *H. sanguineus* along the US east coast was generally accompanied by a massive decrease of *C. maenas* (Lohrer and Whitlatch 2002; Kraemer et al. 2007; O'Connor 2014). Likewise, *H. sanguineus* was found to be highly mobile (Brousseau et al. 2002) and it dominated *C. maenas* in competition for food and shelter (Jensen et al. 2002).

Metabolic energy expenditure

The total energy expenditure per site and species is obviously dependent on the density and biomass of the crabs. Considering the biomass values of August 2014, the energy expenditures for *C. maenas* and *H. sanguineus* are in the same order of magnitude for each site. Consequently, the August values for the entire Helgoland intertidal zone are similar, even if the biomass of *H. sanguineus* is generally lower than that of *C. maenas* (Table 1). The energy expenditure of *C. maenas* exceeds that of *H. sanguineus* during most of the year, but it is similar during summer. Due to the absence of *C. maenas* from the intertidal area in winter (see "Materials and methods"), the cumulative energy expenditure of the two species for the whole year 2014 was very similar. Generally, the energy expenditures calculated for both species are first assessments, as these laboratory measurements could not consider field conditions such as locomotory activity, photoperiod or exposure to air during low tide that might have an influence on metabolic rates (e.g., Dehnel 1958; Taylor et al. 1977).

The energetic expenditure of the crabs is relatively small compared to the total primary production in rocky intertidal areas. The annual carbon uptake of *C. maenas* and *H. sanguineus* in the Helgoland intertidal ranges between 2.1 and 2.6 g C m^{-2}, and between 2.2 and 2.8 g C m^{-2}, respectively (derived from the cumulative energy expenditure for 2014). Unfortunately, no primary production data are available for the Helgoland intertidal area. For kelp forests, as for example present in the subtidal area around Helgoland, a value of about 2 kg C m^{-2} year^{-1} is established (Thomas 2002). For a similar rocky intertidal region, the Ria of Vigo (northwestern Spain), a value of 416 g C m^{-2} year^{-1} was reported (Niell 1977). A Wadden Sea intertidal sand flat had a primary production of 81.2 mg C m^{-2} d^{-1} and a consumption of 0.84 mg C m^{-2} d^{-1} for *C. maenas* (Baird et al. 2004). Both examples indicate that primary production is not a limiting resource in intertidal areas.

The Helgoland population of *C. maenas* is not or not yet suffering from the invasion of *H. sanguineus*, since the abundance of both crab species together in the Helgoland intertidal roughly doubled from 2009 to 2014. However, abundances of *H. sanguineus* around Helgoland may continue to increase (Jungblut et al. 2017). A considerably higher density of *H. sanguineus* may then have stronger effects on the community patterns in the rocky intertidal. The ecological impact of *C. maenas* on this area was previously described as rather limited (Janke 1990). The feeding ecology of *H. sanguineus* around Helgoland is not yet fully understood. If both species are opportunistic omnivores, competition for food can be expected (e.g., Ropes 1968; Tyrell and Harris 1999; Lohrer et al. 2000b; Griffen et al. 2012). If *H. sanguineus* prefers an herbivorous diet, competition would

be less pronounced, but *H. sanguineus*' energy expenditure would exceed that of *C. maenas*. However, macroalgae are not a limiting resource in the Helgoland intertidal.

In the nearby Wadden Sea, another invader, the Asian brush-clawed shore crab, *Hemigrapsus takanoi*, is also present in high abundances in addition to *H. sanguineus* and *C. maenas* (Landschoff et al. 2013). Here, competition for food could be stronger and more complex, as macroalgae are not very abundant in the Wadden Sea intertidal zone. Energy flow models of this region should be updated to account for the impact of those successful invasive crab species (Baird et al. 2004, 2007, 2012).

Conclusions

Since 2007, *Hemigrapsus sanguineus* has successfully invaded the rocky intertidal around Helgoland and established a prospering population. Abundance and biomass of the invader have reached values as high as 21 and 59%, respectively, of those recorded for the native *Carcinus maenas*. However, depending on the diet, the energy expenditures of the invader reached 80–125% (for August 2014) and 86–135% (for the whole year 2014) of the values calculated for the native crab. Energetic requirements of *H. sanguineus* in their new habitat are thus in the same range as those of *C. maenas*.

Present warming trends in Helgoland waters attributed to climate change (Wiltshire and Manly 2004) and the fourfold higher warming projection for the North Sea, compared to the global average (Belkin 2009), will most likely be favorable for *H. sanguineus*. Increasing ambient temperatures may accelerate its growth and facilitate reproduction. Furthermore, increasing human influence and subsequent alterations in coastal habitats such as the creation of artificial hard substrate are also known to promote non-indigenous species in competitive situations (Byers 2002; Bulleri and Chapman 2010). Consequently, we predict that the overall energetic impact of *H. sanguineus* will increase, while asserting competitive dominance over its native ecological equivalent *C. maenas*. To assess the ecological influence of the invader more comprehensively, subsequent studies on, e.g., dietary preferences and competitive interactions are needed. Prevalence of the invader will eventually have implications for the original community patterns in rocky intertidal areas. Studies of the community impact of *H. sanguineus* in invaded habitats are, however, still pending.

Compliance with ethical standards

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